

# ABYSSAL ASCIDIANS COLLECTED FROM THE PROXIMITY OF HYDROTHERMAL VENTS IN THE PACIFIC OCEAN

Claude Monniot

## ABSTRACT

Repeated dives of submersibles in remarkable areas of the ocean such as rifts, hydrothermal vents, and trough slopes have provided faunal samples attached to rocks. During six oceanographic cruises eight ascidian species were collected from such sites. Three species described here are new, three others are completely redescribed, and two have their geographical distributions extended. In addition, *Benthascidia michaelseni* is revised after a new study of the type material.

The discovery of hydrothermal vents has stimulated the exploration of oceanic rifts and troughs. Tunicates are sometimes abundant along rift axes, near vents, or on fossil sites. These tunicate species, often large and sometimes very brittle, cannot be collected by trawls or dredges which are poorly suited for collecting on deep rocky bottoms. Deep sea ascidians that settle on rocks are therefore poorly known. Some species have been found on polymetallic nodules, pumice, stones or pieces of rocks, but very fragile species can be only collected in good condition with submersibles.

In this report, I present descriptions of species collected from the Pacific Ocean during recent American, German, and French cruises.

## ASCIDIAN SOURCES

Material from the Escabana Trough of the southern Gorda Ridge, cruise L1-86-NC of the RV S.P. LEE was collected by a team from Oregon State University with a dredge during dive 558 of the D.S.V. SEA CLIFF. These specimens were sent to us for study by Dr. Andrew G. Carey, Jr.

Material from the Eastern Pacific Ridge, collected by the DSV ALVIN and the Woods Hole Oceanographic Institution, were sent to us for study by Dr. Cindy L. Van Dover.

Material from the Northern Trough of Peru was collected by the submersible NAUTILE during the NAUTIPERC cruise. These specimens were sent to us by the Centre National de Tri d'Océanographie Biologique (CENTOB/IFREMER).

Material from the Japan Trough was collected by the submersible NAUTILE during the Kaiko-Nankai cruise to the eastern Nankai accretionary wedge and the sample sent to us by CENTOB.

Material from the Tres Marias Trough and El Gordo Volcano, (Manzanillo and Tecpan basins, Mexican Pacific) collected by the submersible NAUTILE during the NAUTIMATE cruise was sent to us by CENTOB.

Material from the Aleutian Trench, cruise SO 110/1b of the RV SONNE was collected by a team from GEOMAR (Research Center for Geomarine Science) with a TV-Guided grab and sent to us by Heiko Sahling.

For taxonomic study, the tunic of specimens preserved in formalin was removed. The body wall was cut along the ventral line and pinned in a dissecting device in tap water. The whole animal was then progressively stained with hemalum to facilitate the next dissection. The branchial sac was removed and mounted on slides in a plastic medium to obtain a permanent preparation.

## SYSTEMATICS

Family Cionidae  
*Ciona mollis* Ritter, 1907  
(Fig. 1)

Mexican Pacific, Tres Marias Trough. NAUTIMATE diving cruise of the DSV NAUTILE Dive 13, sample 3 20°57'N, 106°19'W, 4370 m.

**Description**— In the tunic, the contracted specimen measures  $8 \times 3 \times 3$  cm. It was attached by the posterior third of its left side to a mudstone that had formed in place on a 20–30° slope. The oral siphon is terminal, somewhat protruding, with 7 indistinct lobes. The cloacal siphon is short, 2 cm from the oral siphon, and has 6 lobes. The tunic is soft, smooth, slightly thickened where it adheres to the substrate. The posterior part of the body, 2 cm long, has a thick tunic without visible blood sinuses.

Removed from its tunic, the contracted body measures  $3.5 \times 2$  cm. The distance between the siphons remains 2 cm. The body wall is soft and translucent. The pattern of musculature is characteristic: 6 strong muscular strands on each side converge to a round area two thirds the way back along the ventral side (Fig. 1A). Each muscle stops abruptly at the edge of this area, where the tunic's blood vessel arises. No special structure of the tunic is to be seen there. There are no other thoracic muscles. On the siphons, thin radial fibers cross circular ones.

The oral tentacles arise from a rather strong muscular band. About 40 of them are arranged in four orders, which alternate dorsally more regularly than ventrally. The tentacles are less numerous than the 225 to 250 counted by Ritter (1907).

The prepharyngeal groove has two high rims where it is farthest from the oral tentacles. The dorsal tubercle bulges and has a dorsoventral slit. (Fig. 1C). The dorsal lamina is made of triangular languets of equal size along its whole length. They arise from a large, imperforate band of the pharyngeal wall. The languets rarely attach to the transverse sinuses on each side of the branchial sac, but rather are linked only to the sinuses on the left side. The endostyle stops well short of the esophagus entrance, and is replaced by two crests. Even with injected stains, it has not been possible to show any pharyngo-epicardic openings in this region. There is no endostylar appendage into the epicardic cavity.

The branchial tissue is thin, without even minute plications (Fig. 1B). The transverse sinuses are narrow, protruding well into the branchial cavity. They carry long, transversely flattened papillae. The papillae are linked by longitudinal sinuses at their bases. Close to their tips, these papillae bud long branches, parallel to the longitudinal vessels, to make, in some places, secondary internal longitudinal vessels.

Ritter (1907: 38) noted “secondary lobes of the papillae”, but he did not see that they might be connected. This kind of structure, with two superposed longitudinal sinuses, has been described in the abyssal antarctic Cionidae *Mysterascidia symmetrica* Monniot and Monniot 1982. The branchial structure of *Ciona mollis* is intermediate between that of the condition in *Ciona* and that of *Mysterascidia*.

The parastigmatic sinuses of *C. mollis* are exactly the same as the transverse sinuses. Ritter (1907) showed very thin parastigmatic sinuses of another second order. They are not present in our specimen. The branchial meshes are twice as long as they are wide and contain 4 to 6 elongated stigmata. The stigmata are 2 to 4 times the width of the tissue

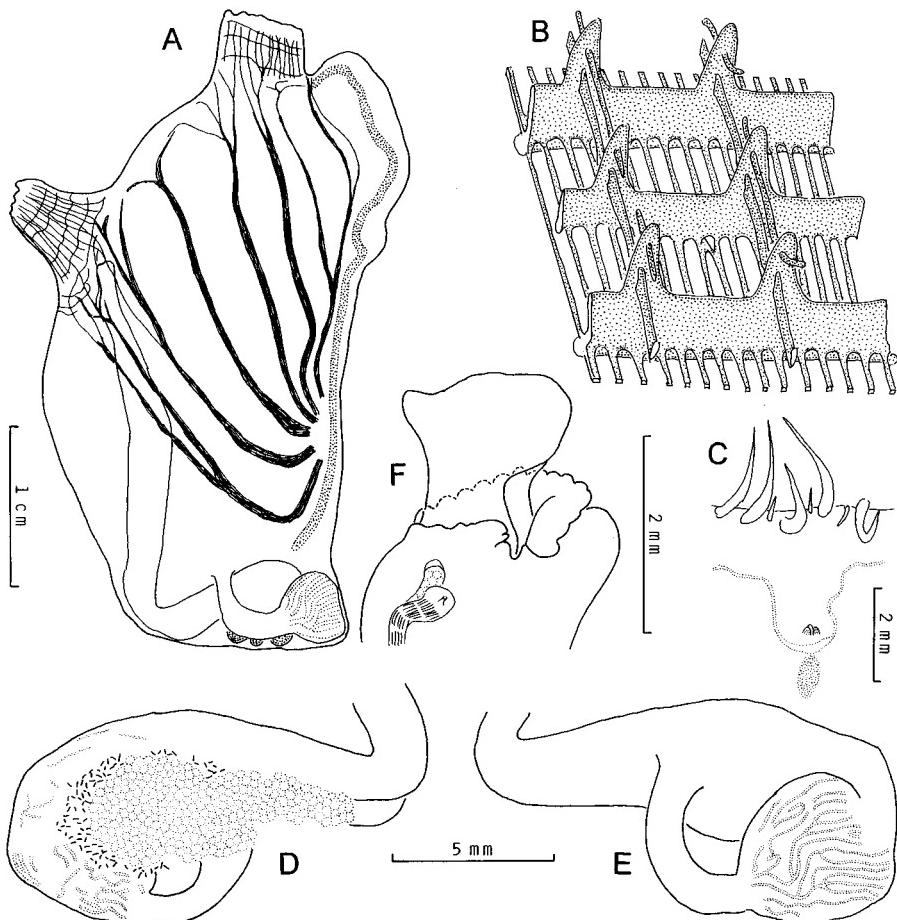


Figure 1. *Ciona mollis*: A, Right side of the body, tunic removed; B, Schematic branchial structure; C, Neural region; D, Left side of the gut and gonads; E, Right side of the gut; F, Anus and extremities of gonoducts.

separating adjacent stigmata. Sometimes, the stigmata are interrupted under the parastigmatic sinuses, but we have not observed any real doubling of the stigmata rows.

For the most part, the digestive tract lies posteriorly to the branchial sac. It forms a horizontal loop curved to the left side. The esophagus is long and curved toward a dilated, thin-walled stomach. The right side of the stomach has more or less sinuous grooves, well-marked and ramifying toward the pylorus (Fig. 1D,E); they are less conspicuous on the left side. The stomach is clearly separated from the wide intestine. The latter's transparent wall reveals whitish and irregular strips in the anterior part, which do not have the same appearance as the stomach grooves. The rectum is long, straight, and attached to the dorsal lamina. It ends in an anus with two fringed and curled lobes. From the anus a rectangular sheet of tissue protrudes (Fig. 1F). This is a prolongation of the intestinal typhlosole and is somewhat reminiscent of the wing-like anal extensions of *Corynascidia alata* Monniot and Monniot, 1991, and *C. cubare* Monniot and Monniot, 1994.

The gonads lie in the intestinal loop. The ovary is especially evident on the left side of the stomach; it extends anteriorly beyond the esophagus entrance (Fig. 1D). The testis acini in this specimen are not well developed around the ovary. The gonoducts end a little short of the anus. They are empty, except for a small mass of sperm at the pore of sperm duct which ends in a single papilla (Fig. 1F).

*Remarks.*—The newly collected specimen corresponds well to Ritter's (1907) samples collected off California (south of San Nicolas Island,  $35^{\circ}15'N$ ,  $119^{\circ}30'W$ , 2000 m depth). The peculiarity of the musculature and of the branchial structure are confirmed here. The only difference is the tentacle number.

*Ciona mollis* is clearly distinct from *C. pomponiae* Monniot and Monniot, 1989 from the Galápagos slope, whose musculature has many transverse fibers and 4 longitudinal ribbons, 2 of which do not reach the end of the body. In *C. pomponiae*, the gonoducts extend beyond the anus and the branchial sac is similar to those of all other *Ciona* species.

Only two *Ciona* species have gonoducts that end before the anus: *C. gelatinosa* Bonnevie, 1896 (arctic and bathyal Atlantic), very close to *C. intestinalis*, and the antarctic *C. antarctica* Hartmeyer, 1911. In the latter, the muscular ribbons tend to group in the postero-ventral angle of the body (Hartmeyer, 1911, pl. 52, fig. 5), but the branchial sac is normal. In addition, that species has a large organ against the gut (Monniot and Monniot, 1983) that is not found in *C. mollis*.

Family Ascidiidae  
*Ascidia escabanae* new species  
(Figs. 2A–C, 3A)

North East Pacific, Escabana Trough of the southern Gorda Ridge. (Cruise L1-86-NC of the RV S.P. LEE) Dredges no. 15D:  $40^{\circ}46.7'N$ ,  $127^{\circ}31.1'W$ , 3260 m; 29D:  $40^{\circ}59.8'N$ ,  $127^{\circ}31.1'W$ , 3230 m. (Holotype from Dredge 29D): D.S.V. SEA CLIFF dive 658/558.

*Holotype.*—USNM 20596

*Paratypes.*—USNM 20597 and 20598 and P5.Asc.A 266 in MNHN collection.

*Description*—The following description has been made from the largest undamaged specimen ( $70 \times 40$  mm), which has apertures 35 mm apart. The animal was attached ventrally with its oral aperture anterior and its cloacal aperture mid-dorsal. The fixation surface has been torn but might correspond to the posterior 2/3 of the ventral region.

The test is thin (1 mm), smooth, and somewhat ridged. The dorsal part is slightly pigmented with brown in its external layer. The tunic is invaded with very conspicuous blood vessels (Fig. 3A) that all arise from the same point on the left side of the body, at the level of the distal bend of the intestinal loop. The vessels branch and spread into the whole test. The siphons are slightly protruding, with longitudinal folds ending in lobes (7 around the oral aperture and 6 around the cloacal aperture).

The body wall is thin and transparent. The muscles are divided into two fields: one along the endostyle and the other dorsal. They are united by fibers lying on the right mantle. Longitudinal fibers extending from the oral siphon fuse with the right-side musculature, and, on the left side, end halfway between the oral siphon and the anterior limit of the intestinal loop.

The oral tentacles form a ring. We have counted about 40 large ones, alternating in 2 or 3 orders, all of a similar length. Some others, very small, are irregularly intercalated. The

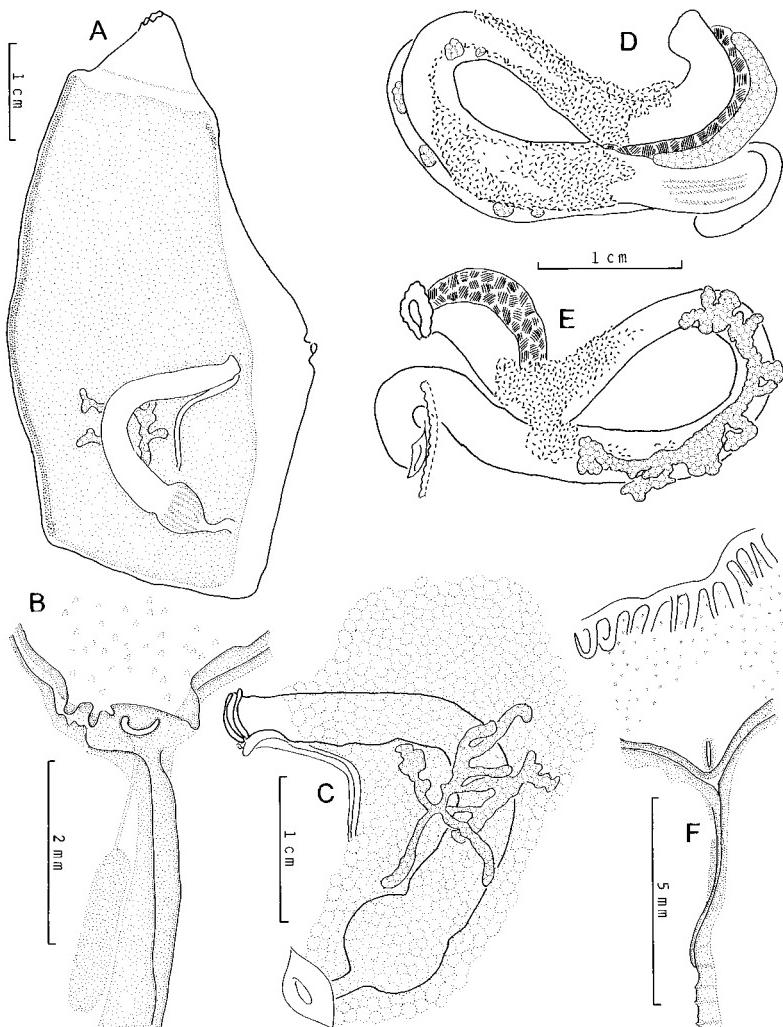


Figure 2. *Ascidia escabaneae*: Left side of the animal without tunic; B, Neural region; C, Intestinal loop with ovary. *Ascidia formella*: D, External side of the gut and gonads; E, Internal side of the gut and gonads; F, Neural region.

peripharyngeal band is made of 2 equally high lamellae with a slight dorsal inflection (Fig. 2B). The dorsal tubercle is U-shaped, with well separated sides, and does not protrude. The neural ganglion is located close to the dorsal tubercle, at a shorter distance from it than its own length. There are thin papillae between the ring of oral tentacles and the peripharyngeal band (Fig. 2B). The dorsal lamina is made of 2 blades in the anterior part; they fuse at a distance from the dorsal tubercle equal to 3 times the length of the neural ganglion. In the median part of its course, the dorsal lamina is high, its edge cut into lappets corresponding to the transverse vessels; these themselves are dentated. The dorsal lamina encircling the esophagus entrance has the same structure. On the right side, at this level, the transverse bars fuse to make a plain and low blade.

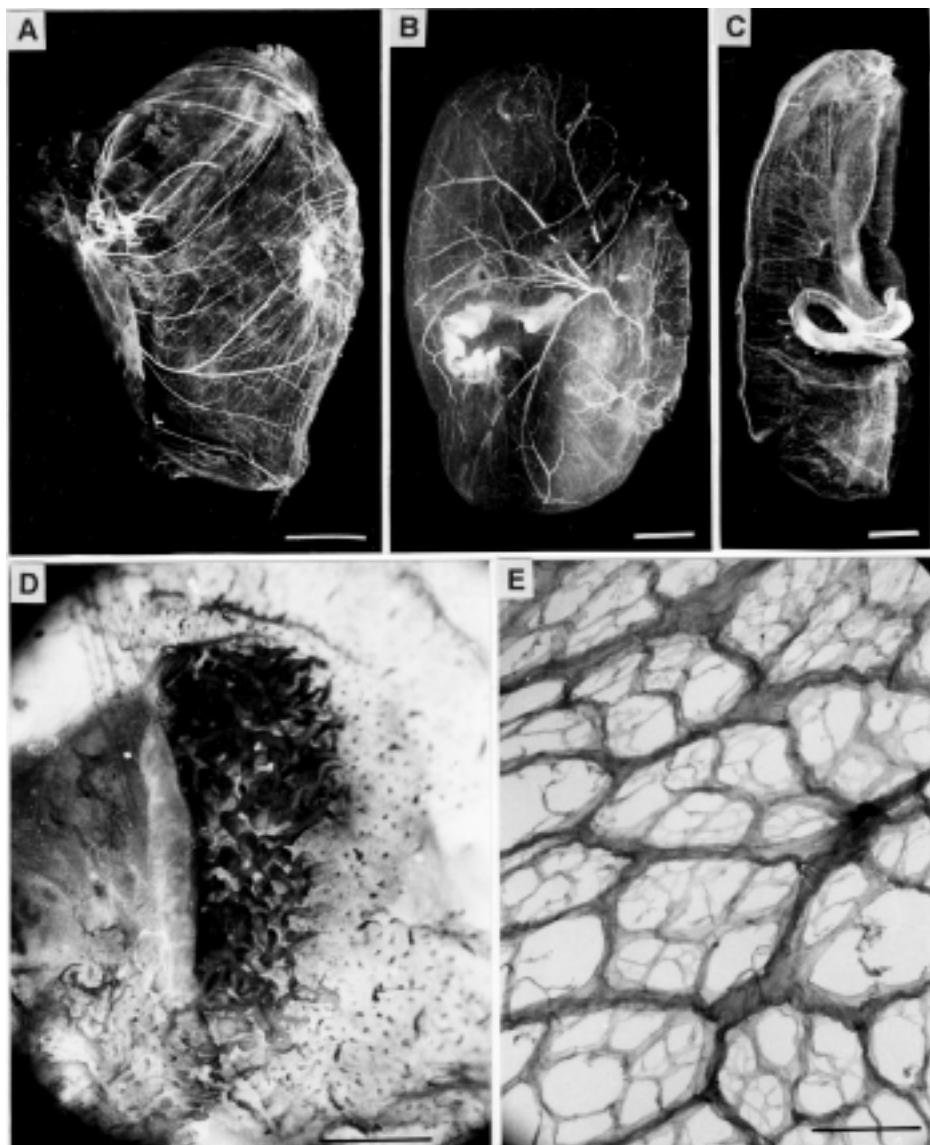


Figure 3. *Ascidia escabanae*: A, Empty tunic. *Ascidia formella*: B, Empty tunic; C, Right side of the animal without tunic. *Kaikoja globosa*: D, Cluster of papillae at the esophageal entrance. *Benthascidia michaelensi*: E, part of the branchial sac. Scale bar A, B, C = 1 cm; D, E = 1 mm.

The branchial sac is thin and flat. At the level of the anterior bend of the intestinal loop, there are about 80 longitudinal bars on each side. They carry digitiform main papillae and smaller secondary ones, but parastigmatic vessels are missing. The mesh size is rather irregular, and each contains 3 to 5 somewhat elongated stigmata.

The gut makes a single, open loop (Fig. 2A,C). On its internal side, it is completely enclosed in a bushy protrusion of accumulation vesicles that spread onto the body wall. The stomach is globular with longitudinal glandular ridges, separated from the intestine by a narrowing of the gut. The anus has 2 lobes.

The ovary (Fig. 2C) is also covered by the mass of accumulation vesicles. It lies on the internal side of the intestine, overlapping the loop. The gonoducts (empty in this specimen) follow the border of the vesicular mass. The genital papillae open at the level of the anus.

The affinities of this species will be discussed after the description of *A. formella*.

***Ascidia formella* new species**  
(Figs. 2D–F, 3B–C)

Mexican Pacific: El Gordo volcanic complex. NAUTIMATE cruise of the DSV NAUTILE Dive 6, sample 4 18°10'N, 104°34'W, 3988 m.

*Holotype*—MNHN P5 Asc.A 267.

*Description*—The specimen measuring  $11 \times 6 \times 3$  cm, was attached to a basaltic rock by its whole left side. The siphons are small, the oral one being terminal, the cloacal siphon in the middle of the right side (Fig. 3B). The tunic is clean and transparent in the living animal. Its whole surface is covered with small papillae corresponding to the farthest ramifications of test vessels. The tunic is thin (1 mm) on the right side and dorsally, and 1 cm thick on the left side. Its internal surface is deeply indented at the gut level, making a deep, almost closed groove, virtually a mold for the digestive tract, hence the species' name.

The oral siphon has 12 inconspicuous lobes, atop a thin membrane. The siphonal musculature is weak, comprising circular and radial fibers that do not extend beyond the level of the oral tentacles. The body musculature is mostly composed of dorsal transverse fibers that make a loose network on the right side and on the dorsal quarter of the left side. The muscles divide and disappear at the endostyle.

About 85 tentacles in 3 size orders arise from a protruding muscular ring. They are long (more than 1 cm), thin but rigid, forming a comb. The prepharyngeal band has 2 thick, low rims, with a dorsal V that is not well marked. The neural ganglion is anterior, close to the dorsal tubercle. The dorsal tubercle is embedded in the body wall, opening by an antero-posterior slit (Fig. 2F). The dorsal lamina begins anteriorly as 2 sheets 5 mm high, combining into a low blade posterior to the neural ganglion. Its rim carries papillae that correspond to the left transverse sinuses. Between the papillae there are irregular denticles. The dorsal lamina encircles the esophagus entrance, becomes lower and the denticles disappear there. There is not special differentiation on the right of the esophagus entrance.

The thin branchial tissue is flat. The transverse vessels have high papillae with 2 lateral extensions. The longitudinal vessels are thin. The meshes, somewhat elongated longitudinally, contain 4 to 5 large stigmata. There are no parastigmatic vessels and no intermediate papillae.

The gut (Fig. 3C, 2D, E) lies about two thirds of the way posteriorly along the length of the body. The loop is rather horizontal and narrow: the secondary bend is not well marked. The gut protrudes like a hernia as it inserts into the groove in the tunic here. All the space between the intestinal limbs is occupied by tunic. The esophagus is curved as it penetrates the tunic. The stomach is only slightly widened; it has glandular grooves only on its external side against the tunic. The cylindrical intestine ends in a widened anus with fringed lobes.

The ovary is sausage-shaped, a little ramified on the internal side of the intestine (Fig. 2E). Some ovarian lobes can be seen on the external side, mostly outside the gut loop. The testis acini lie on both sides of the gut and are more abundant where the intestine tends to approach the stomach. Each gonoduct, full of gametes, opens by a simple papilla close to the anus. The accumulation vesicles are small, difficult to see and do not contain concretions.

*Remarks.*—Ascidians which belong to shallow water genera generally show a reduced size in deep water. But deep *Ascidia* species, which are not numerous, are rather large with a small gut compared to the size of the branchial sac.

These 2 species present important differences in gut shape and gonad disposition, but they show real affinities with each other and with the two bathyal *Ascidia* known in the eastern Pacific: *A. clementea* Ritter, 1907 from 1000 to 2000 m off California (but at only 375 m near the Galápagos Islands), and *A. fusca* Monniot and Monniot, 1989 taken from 335 m on the Galápagos slope.

These species have in common a tunic with a network of blood sinuses; a prebranchial area covered with small papillae; a dorsal tubercle of a very simple shape with a neural ganglion close by (except in *A. fusca*, where it is distant by three times its length); and a dorsal lamina with 2 sheets anteriorly and somewhat posteriorly to the neural ganglion. They clearly differ by: the gut shape that forms a crescent in *A. escabanae* n. sp. and is partly embedded in the tunic in *A. formella* n. sp.; the disposition of the ovary (a network in the primary gut loop in *A. clementea*, a compact mass in *A. fusca*, a fan-shaped structure on the internal side of the intestine in *A. escabanae* n. sp., and a sausage-shaped organ in *A. formella* n. sp.); and the size and abundance of the accumulation vesicles, which are very developed in *A. clementea* and *A. escabanae* n. sp., but reduced and almost invisible in *A. fusca* and *A. formella* n. sp.

The gut of *Ascidia escabanae* n. sp. has the same shape as that of *A. bathybria* Hartmeyer, 1912, a species known from three specimens collected southwest of Australia, south to the Kerguelen Islands and in the south part of the Angola basin (Monniot and Monniot, 1977 and 1985). Both species have the same prepharyngeal band and dorsal lamina but they differ in many other ways: (a) The oral tentacle number is much higher in *A. bathybria* (more than 100), even though the body size is smaller: only 27 mm long. (b) The interval between the tentacles and the prepharyngeal band is divided into 2 parts by a velum in *A. bathybria*. In *A. escabanae* there is no velum but there are papillae here. (c) The anterior part of the dorsal lamina is doubled in *A. escabanae* but not in *A. bathybria*. (d) *A. bathybria* has only about 30 longitudinal branchial bars on each side instead of 80 (but this may be linked to body size). It has parastigmatic vessels on intermediate papillae. (e) *A. escabanae* has a well-differentiated stomach. (f) *A. bathybria* has a globular ovary encircled by dense testis acini located in the center of the intestinal loop (this is especially conspicuous in the Angola basin specimen), but the ovary of *A. escabanae* is made of tubules that spread over the intestine itself. (g) *A. escabanae* has numerous large accumulation vesicles which cannot be seen in *A. bathybria*.

While *Ascidia escabanae* and *A. clementea* seem closely allied, *A. bathybria* is considerably more different from them. The crescent shape of the digestive tract appears to be a convergence shared by *A. bathybria* and *A. escabanae*.

In the Phlebobranchia it is not exceptional to find the gut embedded in a depression of the tunic. It is the rule in the family Plurellidae, and it happens in such Ascidiidae as *Phallusia mammillata* and *Ascidia capillata*. *Ascidia tritonis* Herdman, 1883, a bathyal

species of the eastern Atlantic, has a cavity in the tunic facing the gut (Monniot, 1969) but it is much less pronounced and the gut shape is very different. This excludes the possibility that *A. tritonis* and *A. formella* n. sp. are the same species.

Family Octacnemidae

***Kaikoja globosa* new genus, new species**

(Fig. 3D, 4A–B)

Northwest Pacific: Nankai accretionary wedge. Kaiko-Nankai diving cruise of the DSV NAUTILE Dive 5, sample 1 33°49'31"N, 137°54'21"E, 1978 m.

*Holotype*.—MNHN P6 Kai 1.

This species shows original characters, some of them already described in *Benthascidia michaelseni* Ritter, 1907, a species with a doubtful taxonomic position. The two type specimens of this species were reexamined, and a new description, unfortunately incomplete because of the poor condition of the types, and a new interpretation are given here. This account will then discuss and compare the genera *Kaikoja* and *Benthascidia*.

*Description*.—The single specimen was found on a block of cemented *Calypogenia* shells, taken near the top of the Yukie ridge on the Northwestern edge of the Nankai trough, in a region with a fossil hydrothermal leak (0.34 Ma–0.78 Ma) (Lallemand et al., 1992). In situ, the spherical animal was attached, without peduncle, close to an alcyonarian on a block about 30 cm across, with its oral aperture oblique but oriented upwards. On the videotape of this capture, the animal is colorless except for a white line (the endostyle) on its upper part. The oral opening looks circular but is made of two basket-like surfaces, one ventral and one dorsal. The visible endostyle indicates that the animal is attached with the dorsal side downwards. When collected, the ascidian was damaged; its oral aperture was cut, and the body was protruding from its test. The test is naked and transparent, without ornaments, and lacks any peculiar vascular system.

Divested of its test, the body shows clearly the disposition of the oral siphon into two flap-like lips. The circular muscles converge at the lips' corners. The fibers are thin and closely packed near the edges of the lips, thicker and more widely spaced posteriorly. They do not extend beyond the circle of oral tentacles. No longitudinal muscles were seen. Inside the cavity formed by the lips many small papillae are scattered anteriorly to the oral tentacles. Several hundred foliate tentacles, each with the shape of a heart or a fan, arise along a ring that encircles this cavity. When they roll up they take on a crescent shape (Fig. 4A). Their size is variable; some of the largest lie a little more anteriorly than the others. The peripharyngeal band is wide, at some distance from the tentacle ring. It is deeply indented where it joins the endostyle. The dorsal part of this cavity, with the neural ganglion, was torn away in this specimen.

In this animal the branchial sac is in shreds. It has only irregular, unciliated holes (Fig. 4B). The perforations are oval, with their main axis longitudinal. On the external side of the branchial sac lies an irregular net of large, soft blood sinuses. On the internal side arise numerous small, soft papillae, which do not take more hemalum stain than the basal tissue, and some other papillae 0.2 to 3 mm long, less numerous, that stain deeply with hemalum. Generally these latter papillae arise opposite the crossings of the external sinusoidal net. The perforations of the branchial sac do not reach the peripharyngeal band, and the space left between the perforated surface and that band carries both kinds of papillae.

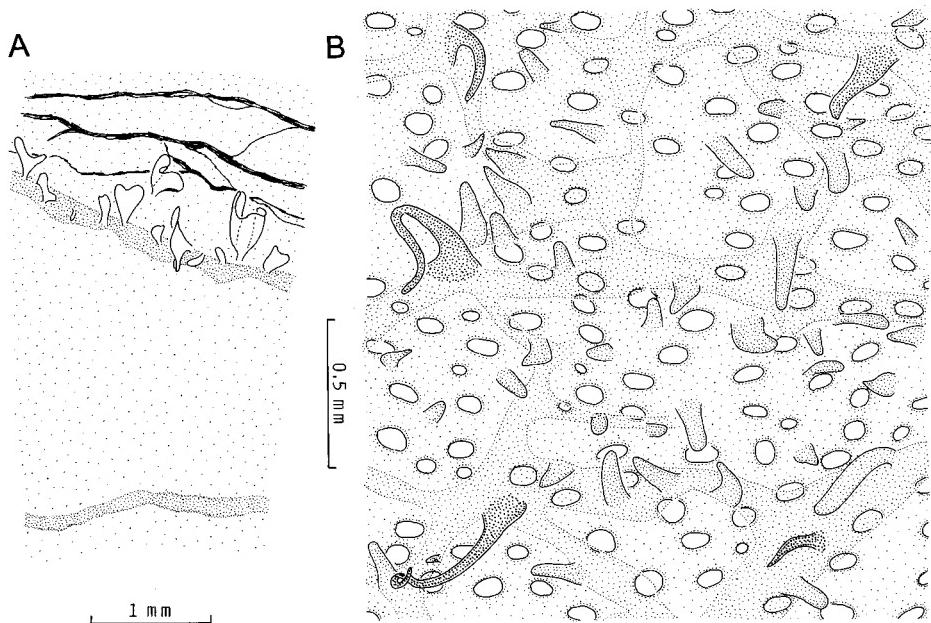


Figure 4. *Kaikoja globosa*: A, Part of the tentacular ring and prepharyngeal groove; B, Part of the branchial sac.

The esophagus entrance makes a slit at the bottom of the branchial sac. The endostyle ends at the ventral side of this slit; the right side of the slit is raised into a thick fold; the left side is covered with a cluster of large, soft papillae arising partly in the branchial sac and partly in the esophagus (Fig. 3D). This cluster is similar to that described by Ritter (1907) in *Benthascidia michaelensi*. Ritter interpreted it as a condensed dorsal lamina at the esophagus entrance. This hypothesis is plausible, as no branchial differentiation exists dorsally close to the esophagus.

The poorly preserved gut makes a simple loop. The flat and wide esophagus opens into a stomach whose wall seems interiorly plicated. The intestine ends anteriorly of the esophagus in a lobate anus. The ovary, with some large eggs, lies in the center of the intestinal loop. The testis overlaps the gut and extends onto the body wall. The specimen's full sperm duct opens at the level of the anus, but it does not follow the intestine. It has not been possible to examine the gut content to determine the diet of this species.

#### Further description of *Benthascidia michaelensi* Ritter, 1907 (Fig. 3E)

Reexamination of the two type specimens lets us correct and add some information to Ritter's original description. Ritter misunderstood this animal's general body shape. He mistook the cloacal aperture for the oral one, and thought the oral siphon was merely a torn part: "The specimens were curiously broken in almost exactly the same way". The body actually is funnel-like, an obliquely cut inverted cone. The narrow base of the conical body is prolonged as a large peduncle 22 cm long, ending in a hairy tuft of branching

and anastomosing processes. The cone itself, containing the body wall, measures 17 cm dorsally but only 8 cm ventrally. The apparently circular oral aperture measures 12 cm in diameter. The cloacal aperture, 2.5 cm in diameter, does not seem to protrude outside and opens in the middle of the body's dorsal side.

Around the oral aperture, the thin body wall contains only circular muscles. The muscular bundles are thin and close to each other near the aperture and thicker but less dense near the oral tentacle ring, where they anastomose. The muscles are parallel in all the pieces left. It is not possible to know now whether the oral aperture was once simply circular or had two broad lobes. Ritter's fig. 29 has to be reoriented and reinterpreted. For him, the part figuring the muscles is anterior; he shows it as a cone narrowing to make a siphon. This interpretation is wrong, as also are the lines apparently depicting radial muscles in this cone. The tentacles (b.t.), the peripharyngeal band (g.i.f.), and the "minute processes" (p.i.f.) are drawn correctly, but what he takes to be a "hypophysis" area is in fact a gaping oral siphon.

Ritter's fig. 30 shows irregular branchial holes. In fact, there is a sinus hierarchy as observed in the *Dicopia* and *Situla* genera (Fig. 3D). The widest sinuses are transverse sinuses, as Ritter's fig. 28 seems to show.

The cluster of papillae (Fig. 28 t.?) is real. It is not in contact with the branchial tissue; it does not make a ring but is limited to an area to the left of the esophagus entrance, and not "between the esophageal and anal orifices". Rather, the anus opens on the other side of the cloacal cavity. The regular ridges of the stomach described by Ritter have not been found in this reexamination.

*Kaikoja globosa* and *Benthascidia michaelsoni* have silica granules in the test cells of the oocytes, a characteristic of the family Octacnemidae (F. Monniot et al., 1992).

*Remarks*.—A third species: *Situla multitentaculata* Vinogradova, 1975, collected in antarctic waters in the South Sandwich trough ( $56^{\circ}52'S$ ,  $24^{\circ}58'W$ , 5530–5650 m) has characters in common with these two species: the absence of radial muscles in the oral siphon, the presence of branchial papillae, and a bush of tentacles at the esophagus entrance.

The division of the family Octacnemidae into genera is based on different kinds of adaptation to a macrophagous diet. These adaptations result in a hypertrophy of the elements of the oral siphon and the progressive reduction of the branchial sac (Monniot, 1972). A considerable development of the oral region and its division into 8 lobes characterizes the genus *Octacnemus*, while the development of the area anterior to the oral tentacles characterizes the genus *Dicopia* (*Megalodicopia*). In contrast, development of the area between the oral tentacles and the branchial sac and the sac's flattening characterize the *Situla*. We believe that the disappearance of the radial musculature, reducing the ability to close the mouth on prey, and the disappearance of the dorsal lamina, justify a generic distinction of *Kaikoja* and *Benthascidia* from the genus *Situla*. And the appearance of long branchial papillae implies a functional change and justifies the establishment of the genus *Kaikoja* itself, distinct from *Benthascidia*.

*Diagnosis of the genus Kaikoja*.—Feminine genus, after the "Kaiko", French-Japanese cruises that collected the species, adding "oja", the Japanese common name for ascidian. Octacnemidae with a circular oral opening or with two lobes, devoid of radial musculature; foliated oral tentacles in a line far from the branchial sac; flat branchial structure, with irregular perforations and a network of anastomosed sinuses with two types of papillae, short and long ones; dorsal lamina absent or replaced by a bush of papillae at the esophagus entrance.

Type species.—*Kaikoja multitentaculata* (Vinogradova, 1975)

*Kaikoja globosa* n. sp. differs from *K. multitentaculata* by the absence of peduncle, the presence of two oral lips with corners marked with an obvious convergence of the circular muscles.

Family Styelidae

*Cnemidocarpa bythia* (Herdman, 1881)

Northern Peru trough, NAUTIPERC cruise of RV NADIR, dive no 1-9-2 of the DSV NAUTILE: 5°35.2'S, 81°53.5'W, 5040 m.

This species, described from the southern Indian Ocean (42°42'S, 134°10'E, 4575 m) has been recorded again in the northern Indian Ocean, widely in the Atlantic Ocean, around Antarctica, in the Tasmanian Sea, and in the Kermadec trough down to 7000 m depth. Its presence in the Northern Peru trough suggests that its distribution also encloses the Pacific ocean.

This small species (4 to 6 mm in diameter) is generally fixed on solid substrata: rocky bottom, loose blocks, polymetallic nodules and plates, and shells.

Family Pyuridae

*Bathypera ovoida* Ritter, 1907

Northeast Pacific, Escabana Trough of the southern Gorda Ridge axial valley. Cruise L1-86-NC of the RVS. P. LEE, dredge no. 3D: 40°45.5'S, 127°30.5'W, 3260–3180 m.

Northern Peru trough, NAUTIPERC cruise of RV NADIR dive no 1-9-2 of the DSV NAUTILE: 5°35.2'S, 81°53.5'W, 5040 m.

Both specimens were damaged. It was not possible to number the branchial folds of the Gorda Ridge specimen. More than 6 are present in the Peruvian animal, which thus cannot belong to *B. splendens*. *B. ovoida* occupies a large bathymetric range. It has been recorded at 5000 m off Peru, 2000 m along the California slope, 180 m in Sagami Bay (Japan) and only 100 m depth in British Columbia. The Antarctic species *B. splendens* is also eurybathic, living from 50 to 5000 m deep.

*Bathypera ovoida* is probably abundant in the Northeastern Pacific. Ritter described the species from more than 100 specimens collected in a single dredging. Pictures taken by submersible along the Gorda Ridge show numerous white spheres attached to rocks that were not collected. They probably represent this species, as its test is covered with white calcareous spicules that reflect the submersible's lights.

*Culeolus gigas* Sluiter, 1904 ?

(Fig. 5A–D)

*Culeolus gigas* Sluiter, 1904: 102, pl.1, fig.1; pl.12, fig.1–3; 3°S–131°E, 924 m; Monniot, F. et al., 1990: 583.

East Pacific Rise, ALVIN dive no. 1996, 18 March 1988, Western Seamount, near 11°29.0'N, 103°53.0'W, 2426 m. On the wall of a scarp; surrounding area characterized as basalt lava, 70% covered with sediment.

*Description.*—The contracted body is cylindrical (Fig. 5A) and measures 12 cm in length and 6 cm in diameter; the peduncle is relatively short 17 cm in length and 0.4 cm in diameter. The oral aperture is close to the peduncle. The siphons cannot close and their apertures reach 3 cm in diameter. The dorsal side between the apertures measures about 5 cm.

The specimen was attached to a rocky substrate by a small disk of very hard tunic. The peduncle is made of sclerified tunic. On the body surface the test is thin and soft, pearly inside. There is a mid-ventral crest made of more or less united papillae more developed posteriorly, and on each side a lateral crest starting from the middle of the cloacal aperture and going to the postero-ventral angle, near where the body joins the peduncle. Both lateral crests join the ventral crest on the mid-ventral line. The test is somewhat mammillated and has large ridges. The rim of each aperture is softly undulated. The test surface is covered with small vesicles which give it a velvet quality. The test is light brown in formalin, but the outer layer is covered with black sediment particles and oxides, that lend it a dark brown general color.

The muscles form well-separated bands issuing from the siphons (Fig. 5B,C). The musculature coming from the cloacal siphon is the most developed. The oral circular musculature extends from the level of the dorsal tubercle to the rim of the aperture; it is thick ventrally near the peduncle's insertion. The oral radial musculature is made of about 10 bands on each side. At the cloacal aperture, the circular muscles of the rim are developed only on the ventral side. The cloacal radial musculature is made of 12 to 15 bands on each side, the most dorsal of them joining those of the oral siphon. All muscles are ramified ventrally near the endostyle. There are no longitudinal muscles on the dorsal side of the body wall. The dorsal lamina is lined by 2 strong muscles ramified near the oral siphon.

There are a dozen oral tentacles; they are short, the largest not exceeding 1 cm, and they are only weakly ramified. The peripharyngeal band does not curve at the top of the branchial folds but makes a deep dorsal V. The small, C-shaped dorsal tubercle is anteriorly opened and slightly displaced on the right side. The dorsal lamina is long and carries a series of short, rounded languets, antero-posteriorly flattened.

The branchial sac is reduced to transverse and longitudinal bars and totally devoid of cilia (Fig. 5D). There are 6 folds on each side, the most ventral is only present in the anterior part. We counted longitudinal vessels on the left side as follows:

D.L. 7 (16) 10 (13) 8 (17) 10 (12) 9 (9) 7 (8) 8 E.

As in many pyurids, fold no. 2 is lower than folds no. 1 and 3. The folds are not very high, and at their crests, the longitudinal sinuses are very close together and less developed than the sinuses located between the folds.

The gut makes an open loop (Fig. 5C). The slightly widened stomach bears an hepatic gland made of erect lobes. We counted 4 lobes on each side, of various sizes. On the left side the first lobe overlaps the right side of the endostyle. The intestine has the same diameter around the loop and a thin wall; it is attached to the body wall. The anus is yellow and has thin lobes. It opens at the end of a short, non-attached rectum.

There is one gonad on each side, made of 8 lobes. The left gonad is located outside the gut loop (Fig. 5C). The ovary is sausage-shaped, widened in successive lobes. The testis acini are placed around these lobes. The sperm duct accompanies the ovary and ends by a papilla that is longer than that of the oviduct. Each gonoducal papilla is marked by a yellow spot, as is the anus; they open at the edge of the cloacal siphon. The gonad lobes

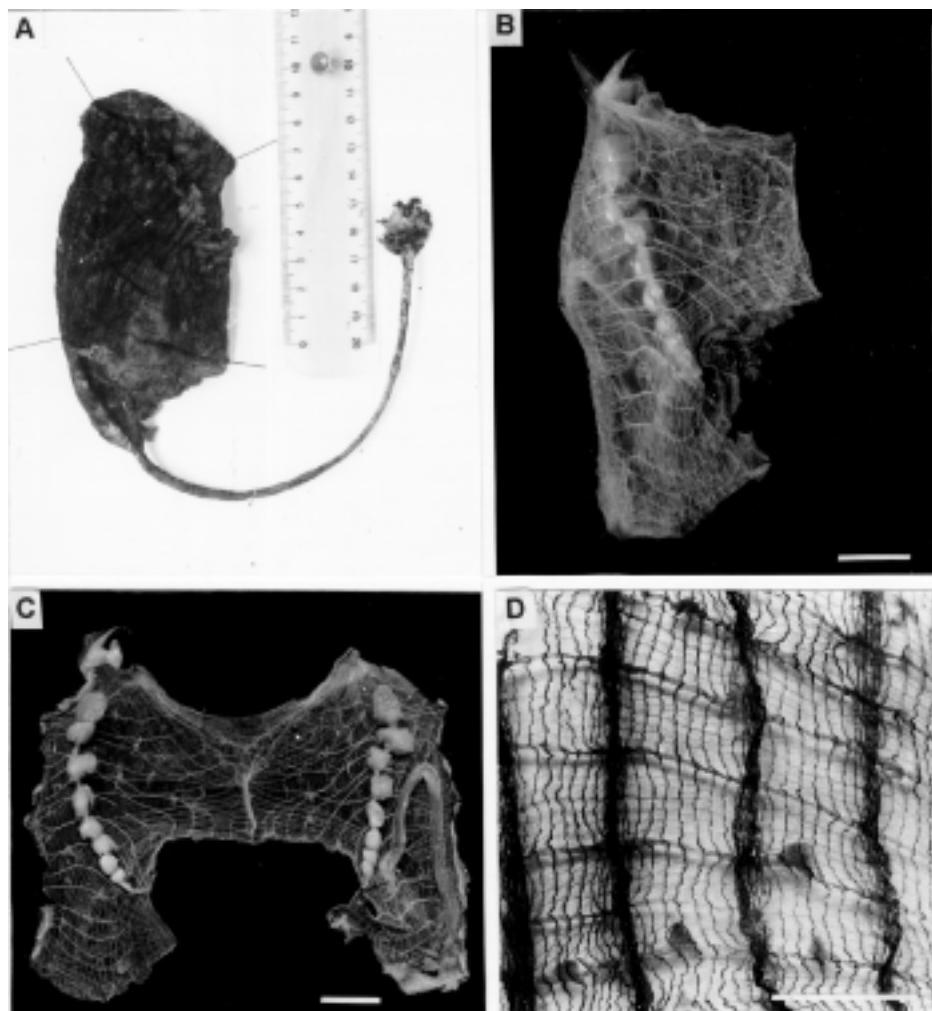


Figure 5. *Culeolus gigas*: A, Habitus right side; B, Left side of the body, tunic removed; C, Internal side of the body, branchial sac removed; D, Four of the six folds of the branchial sac. Scale bar = 2 cm.

are covered by endocarps which are larger the farther they lie from the cloacal aperture. The most anterior endocarps are attached to the branchial sac, the first being fused with the sinuses. There is no cloacal velum.

The heart forms a triangular pouch located near the base of the peduncle. We have not seen any spicule in any tissue.

**Remarks.**—This species is well characterized by its large bulky body on a short, stout peduncle. *C. robustus* Vinogradova, 1970 from the Kurile trough has a similar appearance but is much smaller (4.1 cm). The two species differ in their gonads: in *C. robustus* there are 2 on each side, short and with 1 to 3 lobes apiece. Moreover, *C. gigas* is well characterized by the location of its left gonad, outside the gut loop, although the location of the left gonads is not indicated in the description of *C. robustus*.

The type specimen of *C. gigas* was not found in the Zoological Museum of Amsterdam. Sluiter described 7 folds on each side with 6 to 8 sinuses between each two folds, and one lobated gonad on each side, but he did not say anything about the position of the left gonad. Sluiter's descriptions are often erroneous, and so a doubt must linger not only about the actual details of the specimen he described from the Siboga Expedition but also about the identification of this new material we have examined from the Eastern Pacific Ridge.

*Culeolus pyramidalis* Ritter, 1907  
(Fig. 6)

North East Pacific, Escabana Trough of the southern Gorda Ridge (Cruise L1-86-NC of the RV S.P. LEE dredge no 15D: 40°47.7'N, 127°31.1'W, 3260 m: 2 specimens, one in poor condition, the second 33 × 21 mm in length with a peduncle of 360 mm; dredge no 29D: 40°59.8'N, 127°31.1'W, 3230 m: 1 specimen 13 mm in length with a peduncle of 190 mm).

Aleutian Trench, cruise SO 110/1b of the RV SONNE, TV-Grab, station no. 28-2, 57°27.25'N, 147°59.67'W, 4867 m. Attached to an empty vestimentiferan tube, at a cold seep.

*Description.*—This description is based on the largest specimen.

The body has the common shape of the genus *Culeolus*, with the oral aperture close to the peduncle and the cloacal aperture far from it. Its external appearance corresponds well to Ritter's drawing in Van Name (1945). The tunic is entirely covered with protruding papillae. Each papilla has a transparent tunic through which granules can be seen. Between the papillae the test is grey and thin. Some larger papillae are found on a transverse line crossing each lateral side of the body and meeting at the ventral line. The peduncle axis is made of a horny substance. The tunic is made of 2 layers, a thin external one with the papillae and with vesicles and a soft internal layer with a mucous consistency.

Crossed muscular ribbons make a regular network in the body wall. The very thin body wall swells into pouches in the meshes between the contracted muscles. Both siphons have an anterior and a posterior lip, joined in strong, muscular corners. Each aperture has a large, thin velum. The oral tentacles are long (up to 17 mm) and doubly ramified pinnate in form; we counted 24 of them in 3 or 4 orders of size that alternate regularly. The prepharyngeal band has 2 equal sides and is not deeply indented on the dorsal side. The dorsal tubercle is protruding; its opening has the shape of an inverted S. The neural gland is elongated but shorter than the dorsal tubercle. The dorsal lamina carries large, foliate, transversally flattened languets.

The branchial sac has 5 or 6 folds on each side. The ventral fold is not easily seen and sometimes exists only in the middle region of the branchial sac, where we count longitudinal vessels as follows:

R.E.1(2)(5)3(8)4(10)3(6)3(8)3DL.

DL.2(12)3(8)3(10)4(8)3(6)2(3)1L.E.

As in many Pyuridae, fold no. 2 is less developed than folds no. 1 and 3. There is not any indication of stigmata; the wall of the branchial sac is reduced to crossed longitudinal and transverse sinuses. The largest meshes may reach 3 × 4 mm. The branchial sac is linked to the body wall by large trabecular strands.

The digestive tract forms an open loop. The stomach is a tube with 6 cauliflower-shaped hepatic lobes protruding on each side. The intestine is attached to the body wall. The

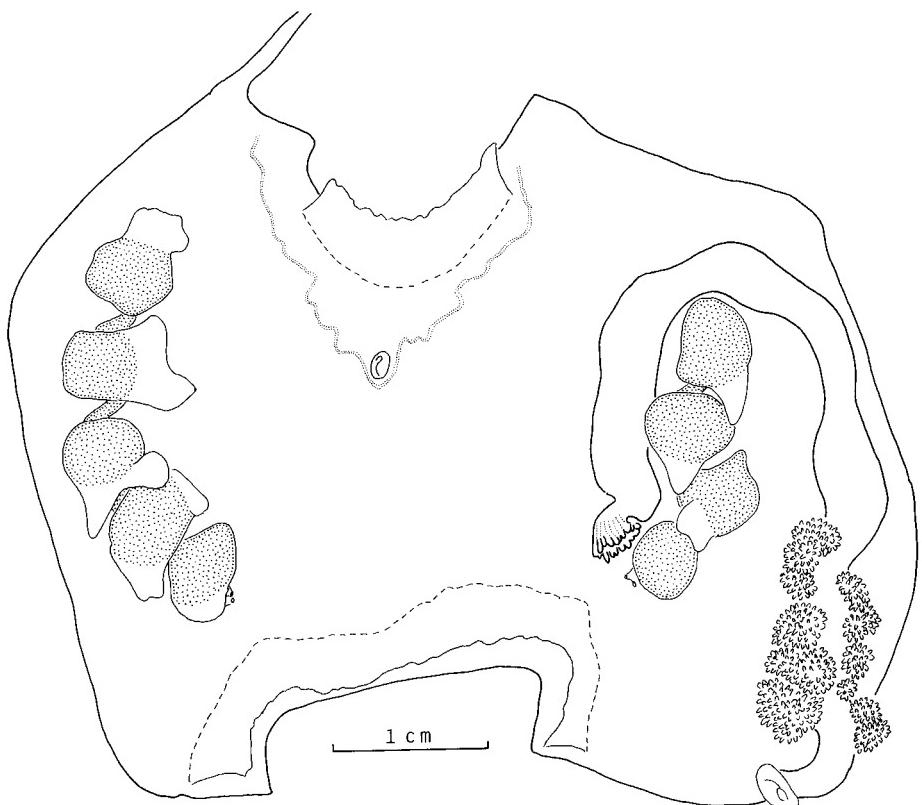


Figure 6. *Culeolus pyramidalis*: Internal side, branchial sac removed.

rectum is short and lies free in the cloacal cavity. It ends in a bilobed anus, each lobe of which is divided in lobules. The lobules are prolongations of ridges along the rectum (Fig. 6).

There is one gonad on each side. The left one, with 4 lobes, is located in the gut loop; the right one has 5 lobes. Each lobe is almost spherical and encloses a testis and an ovary. The lobes carry endocarps. The genital ducts of each gonad open together on a short papilla that is often hidden under one of the gonad's lobes.

We have not observed the spicules described by Ritter.

*Remarks.*—*C. pyramidalis* is known from 3 specimens described by Ritter (1907), collected west of San Diego at the foot of the continental slope ( $32^{\circ}54'N$ ,  $121^{\circ}15'W$ , 4132 m, and  $33^{\circ}01'N$ ,  $121^{\circ}32'W$ , 4075 m). Ritter was not certain that all three specimens, one much larger than the other two, belonged to the same species. His written description is quite thorough but only deals with the one large specimen, which is the only one he depicts (pl. 2, figs. 21–22, external appearance only). This illustrated, described specimen must be considered as the holotype. Millar (1954) briefly described 2 specimens dredged off Acapulco, Mexico ( $9^{\circ}23'N$ ,  $89^{\circ}33'W$ , 3570 m), and specified one gonad on each side. He depicts in a sketch part of the gut. As the external aspect was drawn by Millar's identification may have been swayed by it.

There are only 4 other *Culeolus* species having only one lobulated gonad on each side: *C. thysanotus* Sluiter, 1904; *C. antarcticus*, Vinogradova, 1962; *C. caudatus* Monniot and Monniot, 1991a; and *C. gigas* Sluiter, 1904 redescribed here.

*C. pyramidalis* is closely allied to *C. antarcticus*: both species have the same shape of the gut and gonads. They are distinguished by the posteroventral crest (made of independent papillae in *C. pyramidalis* and united ones in *C. antarcticus* Monniot and Monniot (1982) and the absence of the ventral crest. The branchial sac is also different: there is no rudimentary ventral fold nor any lowering of the sinus number in the second fold of *C. antarcticus*.

*C. thysanotus*, from the Indonesian slope, has a peculiar look of its own, with a tunic entirely covered with large papillae.

*C. caudatus* can have two gonads on the left side. The peduncle axis is not horny but its stiffness is ensured by encrusted sand grains.

## DISCUSSION

The deep tunicate fauna is known essentially from soft bottoms. The species diversity is high. For example, about fifty species are recorded below 2000 m in the Bay of Biscay. Spectacular forms and surprising adaptations have been discovered in the 30 past years Monniot and Monniot (1978). The most striking adaptations are the result of an evolution of species feeding on suspended particles carried by currents flowing passively through them (not generated by branchial cilia), or of carnivorous species that have been transformed into traps that take large prey. These ascidians are not common on abyssal plains, as they need a solid surface to settle on. In recent years, since the hydrothermal vents were discovered, biologists have used submersibles and collected and described some large and remarkable ascidians (Monniot and Monniot, 1989, 1991). The present paper indicates that, although tunicates have not been found very close to the vents, the bathyal and abyssal ascidian fauna of rocky bottoms is varied, and numerous species with puzzling adaptations are being discovered.

No protochordates have been recorded from areas rich in hydrogen sulphide and methane, that is to say in close proximity to vents or cold seeps. However, it is likely that the increases of organic matter near vents and cold seeps are favourable to the development of ascidian fauna, and especially actively feeding species such as those of the genera *Ascidia*, *Ciona*, or *Bathypera*.

## ACKNOWLEDGMENTS

The authors thank A. G. Carey, Jr., who provided the Gorda Ridge material, C. L. Van Dover for the ALVIN material, the CENTOB/IFREMER for the NAUTILE material, H. Sahling who provided the Aleutian Trench material, and the Smithsonian Institution for loan of *Benthascidia michaelensi* type specimens. We highly appreciated the comments and language corrections by T. Newberry.

## LITERATURE CITED

- Hartmeyer, R. 1911. Die Ascidiens der deutschen Südpolar-Expedition 1901–1903. Deutschen Südpolar-Exped. 2: 407–606.  
\_\_\_\_\_. 1912. Die Ascidiens der deutschen Tiefsee-Expedition. Deutschen Tiefsee-Exped. 7: 223–392.

- Lallemand, S. E., G. Glaçon, A. Lauriat-Rage, A. Fiala-Médioni, J.-P. Cadet, C. Beck, M. Sibuet, J. Toshimichi Iiyama, H. Sakai and A. Taira. 1992. Seafloor manifestations of fluid seepage at the top of a 2000-metre-deep ridge in the eastern Nankai accretionary wedge: Long-lived venting and tectonic implications. *Earth and Planetary Sci. Let.* 109: 333–346.
- Millar, R. H. 1964. Asciidae: Additional material. *Galathea Rep.* 7: 59–62.
- Monniot, C. 1969. Ascidies récoltées par la "Thalassa" sur la pente du plateau continental du golfe de Gascogne: (3–12 Août 1967). *Bull. Mus. natl. Hist. nat.*, Paris (2), 41(1): 155–186.
- \_\_\_\_\_. 1972. *Dicopia antirrhinum* n. sp. ascidie de la pente du plateau continental du golfe de Gascogne. Interprétation nouvelle de la famille des Octacnemidae. *Cah. Biol. Mar.* 13: 9–20.
- \_\_\_\_\_. and F. Monniot. 1977. Quelques ascidies abyssales du sud-ouest de l'océan Indien. *Com. Natl. Fr. Rech. Antarct.* 42: 305–327.
- \_\_\_\_\_. and \_\_\_\_\_. 1982. Some antarctic deep-sea tunicates in the Smithsonian collections. In *Biology of the Antarctic Seas*. 10. *Antarct. Res. Ser.* 32: 95–130.
- \_\_\_\_\_. and \_\_\_\_\_. 1983. Ascidies Antarctiques et Subantarctiques: Morphologie et biogéographie. *Mém. Mus. natl. Hist. nat.*, Paris (n.s.), A 125: 1–168.
- \_\_\_\_\_. and \_\_\_\_\_. 1985. Nouvelles récoltes de tuniciers benthiques profonds dans l'océan Atlantique. *Bull. Mus. natl. Hist. nat.*, Paris (4), 7A(1): 5–37.
- \_\_\_\_\_. and \_\_\_\_\_. 1989. Ascidians collected around the Galápagos Island by the JOHNSON-SEA-LINK Research Submersible. *Proc. biol. Soc. Wash.* 102(1): 14–32.
- \_\_\_\_\_. and \_\_\_\_\_. 1991. Tunicata: Peuplements d'ascidies profondes en Nouvelle-Calédonie: diversité des stratégies adaptatives. Pages 357–448 in A. Cronier, ed. *Résultats des Campagnes MUSORSTOM*, vol. 8.- *Mém. Mus. natl. Hist. nat.*, Paris (A) 151: 357–448.
- \_\_\_\_\_. and \_\_\_\_\_. 1994. Ascidians collected in the Weddell Sea by the RV POLARSTERN (EPOS cruise Leg 3). *Bull. Mus. natl. Hist. nat.*, Paris (4) 16A (1): 13–37.
- Monniot, F., R. Martoja and C. Monniot. 1992. Silica distribution in ascidian ovaries, a tool for systematics. *Biochem. Syst. Ecol.* 20 (6): 541–552.
- \_\_\_\_\_. \_\_\_\_\_ and M. Truchet. 1990. Influence de l'environnement géochimique sur la bioaccumulation des métaux par les ascidies abyssales. *C.R. Acad. Sci.*, Paris (3) 310: 583–589.
- Oka, A. 1918. *Megalodicopia hians* n. g., n. sp., eine sehr merkwürdige Ascidie aus dem japanischen Meere. *Annot. Zool. Japo.* 9: 399–407.
- Ritter, W. E. 1907. The ascidians collected by the United States Fisheries Bureau Steamer ALBATROSS on the coast of California during the summer of 1904. *Univ. Calif. Publ. Zool.*, Berkeley 4: 1–52.
- Sluiter, C. P. 1904. Die Tunicaten der Siboga-Expedition I. Abteilung: Die socialen und holosomen Ascidiens.- Siboga Exped. Monog. 56A: 1–127.
- Vinogradova, N. G., 1962. Ascidiæ simplices of the Indian part of the Antarctic. *Biol. Res. Soviet Antarct. Exped.* (1955–1958) 1: 196–214.
- \_\_\_\_\_. 1970. Deep-sea ascidiants of the genus *Culeolus* of the Kurile-Kamchatka Trench. *Trudy Inst. Oceanol.* 86: 489–512.
- \_\_\_\_\_. 1975. On the discovery of two new species of an aberrant deep-water ascidiacean genus *Situla* in the South-Sandwich trench. *Trans. P. P. Shirshov Inst. Oceanol.* 103: 289–303.

DATE SUBMITTED: June 26, 1997.

DATE ACCEPTED: August 1, 1998.

ADDRESS: *Muséum national d'Histoire naturelle, Laboratoire de Biologie des Invertébrés Marins et Malacologie, CNRS D 0699, 55 rue Buffon, 75005 Paris, France.*